

Reproductive biology and annual population cycle of *Oxyloma retusum* (Pulmonata: Succineidae)*

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Abstract: I studied the reproduction and the population turnover of a succineid land snail living by a small lake in central Maryland. The identity of the snail, deduced from its external characteristics and the genitalia, comes closest to *Oxyloma retusum* (Lea, 1834). The species has a semelparous life cycle. The snails that survive the winter grow and reproduce from late March until the end of June when they reach their maximum size and die off. Their offspring (the spring generation) grow throughout the spring and the summer and reproduce briefly near the end of August. In the fall, the survivors from the spring generation and their offspring hibernate from November until the end of March. Snails mate by shell-mounting. In 89% of pairs, mating was anatomically reciprocal. During courtship, one snail climbs on the shell of a prospective mate and circles the shell to initiate mating. In mating pairs with a shell length difference of more than 1 mm, the smaller snail was always on top. This suggests that one function of shell-circling during courtship may be to help the top snail judge its potential partner's size.

Key words: land snail, genitalia, semelparity, mating, courtship

Oxyloma retusum (Lea, 1834) is one of the most common and widely distributed succineid species of the northeastern U.S. (Hubricht 1985). It is found in the vicinity of lentic and lotic habitats, usually very close to the water (Shimek 1935, Baker 1939, Miles 1958, Hubricht 1985, Lannoo and Bovbjerg 1985). The reproductive organs (Pilsbry 1948, Miles 1958, Franzen 1963, Wu 1993), mating anatomy (Webb 1977b), dispersion (Lannoo and Bovbjerg 1985), and diet (Shrader 1972, Örstan 2006) of *O. retusum* have been studied.

However, no published information is available on the life cycle of *Oxyloma retusum*. Mostly anecdotal information in the literature suggests that the continental North American succineids have semelparous life cycles. For example, Pilsbry (1948) stated that *Novissuccinea ovalis* (Say, 1817) often reached "ordinary" size in one season and Grimm (1971) noted that in Maryland, *O. subeffusa* Pilsbry, 1948 matured in early spring and died off before the summer. Strandine (1941) showed that *N. ovalis* indeed had an annual life cycle in Illinois. The only relevant published information regarding the life cycle of *O. retusum* is Pilsbry's (1948) comment that probably most of the large individuals of *Oxyloma decampi gouldi* (Pilsbry, 1948; synonymized with *O. retusum* by Hubricht 1985) died by the end of the summer and that he could find only half-grown shells in the fall.

Besides Webb's (1977b) work on the mating anatomy of *Oxyloma retusum*, no other research on the reproductive biology of the species has been published. Furthermore,

Webb's (1977b) brief accounts of courtship and whether or not penis intromission was reciprocal seem incomplete and need to be supplemented with more thorough observations.

Pulmonate gastropods have evolved a wide spectrum of lifestyles. A better understanding of the biology of any one species will contribute to the solution of the puzzle of pulmonate evolution. Furthermore, information obtained with common species such as *Oxyloma retusum* could be useful for the development of more effective conservation strategies for less common and endangered succineids, for example, *Oxyloma haydeni kanabensis* Pilsbry, 1948 (Spamer and Bogan 1997–1998). In this paper, I present the results of my studies on the mating biology and the annual population cycle of *O. retusum* in Maryland.

MATERIALS AND METHODS

The study took place along the shore of Lake Churchill, a small (~640 m by ~200 m) lake (39.188°N, 77.280°W) in Germantown, Maryland. Besides a small forest remnant along its eastern shore, the lake is surrounded by a residential neighborhood. The lake is connected by pipes to the nearby, larger Little Seneca Lake in Black Hill Regional Park. Both lakes occupy former agricultural fields and were filled in the 1980s by the damming of Little Seneca Creek that runs through the park.

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During preliminary field trips, I found *Oxyloma retusum* within stands of cattails (*Typha* sp.) at several points along the lake. I selected as the study locations two cattail stands, one at the western shore of the lake and the other about 580 m to the east near the northeast corner of the lake. From April through October both stations were covered with dense growths of cattails, various herbaceous plants, and grasses. The shore of the lake was always muddy and had a layer of decomposing leaves. During the winters the lake often froze.

During the monitoring of the sizes of the snails at approx. 2-month intervals from early April to late October, I collected all the live *Oxyloma retusum* I could find at either one or both of the stations until I had a total of at least 40 snails. The collections were usually done over two days. The snails were brought to the laboratory and the shell length (height) of each snail was measured with calipers. Especially during the spring, the edges of the aperture lips of juvenile snails were thin and fragile and easily crushed by the caliper jaws. Consequently, accurate measurements of shell lengths were difficult and the histograms were constructed using classes 1 mm wide.

The permanent removal of large numbers of live snails, especially from a small population, may modify population dynamics (Heller 2001). Since I did not know the total population sizes of *Oxyloma retusum* at the study locations, to avoid interfering with the natural population cycles, I returned the live snails to their respective stations within a few days, occasionally keeping only a few of the largest snails for dissection. Those were killed in ~5% ethanol and saved in 70% ethanol.

To study their mating, I brought snails to the laboratory in individual containers and kept them isolated from each other except during periods of observation. I kept the snails in small, numbered plastic containers lined with damp toilet paper and fed them dead cattails, tree leaves, and carrots. Although some young snails were kept up to 14 days before they were returned to the field, they did not grow much in captivity.

To induce snails to mate, I placed them in pairs or in groups of three or four in a small container or on a large glass plate held horizontally by a clamp. The advantage of the latter method was that the plate could be rotated, permitting examination and photography of a mating pair from different angles. If the plate was rotated slowly, snails remained attached to it even when upside down. I sprayed water on the plate occasionally to prevent the snails from drying.

To determine if mating was anatomically reciprocal, that is, if each snail in a pair was inserting its penis into its partner's vagina simultaneously, I developed a forced withdrawal method: I gently picked up a pair that had been conjoined for at least about 15 minutes, pulled them apart slightly to disrupt their mating, and then waited for the snails to complete

withdrawing their penises while watching them under a dissecting microscope.

I have deposited two alcohol-preserved specimens of *Oxyloma retusum* in the Field Museum of Natural History, Chicago, Illinois (FMNH 312423, FMNH 312424). Additionally, I have deposited four alcohol-preserved specimens in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CM93115, CM93116, CM96781, CM96782), including one specimen with an everted penis (CM93115) and one specimen in 95% ethanol (CM96781).

RESULTS

Identification

External characteristics

The mantle, especially in the front and along the sides, was densely stippled with small, black spots. But the spots did not form any distinct patterns (Figs. 1-2). The head was light brown. The head and the sides of the foot were also stippled with dark spots. The spots coalesced into longitudinal bands in front of the head between the tentacles (Fig. 3) and formed splashes along the sides of the foot (Fig. 2).

Genitalia

I dissected five snails collected in June 2001, June 2002, June 2003, and May 2008. The general characteristics of the genitalia (Fig. 4) agreed in all specimens. The penis and the epiphallus were encased within a translucent sheath. The vas



Figure 1. A mating pair of *Oxyloma retusum*. The larger snail's shell has a varix (arrow) across its body whorl.

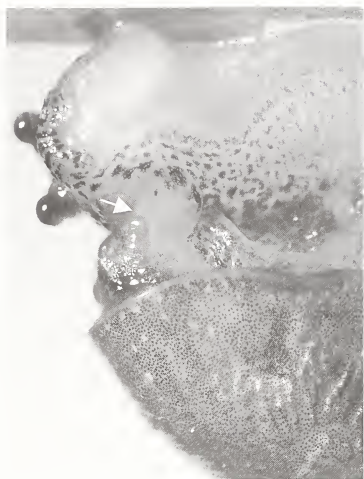


Figure 2. A pair of *Oxyloma retusum* that flipped over the edge of a glass plate after they started mating. The snail that was on top is now hanging below. Arrow is pointing at the junction of the genital openings.

deferens entered the sheath near the retractor muscle (Fig. 4A). The sheath around the epiphallus and the surface of vas deferens, before it entered the sheath, were stippled with black dots. Within the sheath, the epiphalluses of all but one specimen and the penises of two specimens were coiled. An appendix, traditionally taken to be demarcating the penis and

the epiphallus (Pilsbry 1948), was present in all specimens; its approximate length varied from 0.3 to 0.5 mm ($N = 5$). The ratio of the combined lengths of the penis and the epiphallus to the length of the vagina varied from 1.2 to 1.5 ($N = 5$); the smallest ratio was obtained with a specimen in which both the penis and the epiphallus were coiled, while the largest ratio was obtained with a specimen in which neither the penis nor the epiphallus was coiled. The bursa copulatrix had a bulbous bursa (Fig. 4A). The ratio of the combined lengths of the peduncle and the bursa of the bursa copulatrix to that of the penis and the epiphallus varied from 1.1 to 1.6 ($N = 3$). A long retractor muscle originating from the back of the body cavity forked near the vagina (Fig. 4A); one arm of it passed between the penis and the vagina and fused into the right upper tentacle, while the other arm, which was loosely connected to the base of the penis as it passed by it, inserted into the body wall near and to the left of the right upper tentacle.

Five of the snails placed in ~5% ethanol died with their penises everted. The distal ends of four of the penises narrowed down to a finger-like tip that was probably the everted appendix (Fig. 4B). The fifth penis had a blunt end; what appeared to be the uneverted appendix was visible inside the penis. The epiphallus was visible through the translucent wall of each penis and its opening was subterminal when the appendix was everted (Fig. 4B). The surfaces of the everted penises were covered with very small, crystalline, scattered granules. The mean length of four penises, including their everted appendices was 3.88 mm ($SD = 0.27$ mm). The mean length of the four appendices was 0.55 mm ($SD = 0.17$ mm). One specimen (CM93115) that had mated shortly before it was killed had an additional 0.78-mm long, yellow appendage loosely attached to the surface of its penis (ps in Fig. 4B). The everted penis of its mate that was also killed lacked that appendage. The external characteristics and the genitalia

of the snails agreed with the literature descriptions of *Oxyloma retusum* (Pilsbry 1948, Miles 1958, Franzen 1963, Wu 1993).

Mating

The only time I saw mating *Oxyloma retusum* in the field was in May 2008. However, mating pairs were observed many times among the snails brought to the laboratory between late March and early September. The earliest matings took place on 24 March 2006 among the snails collected on the same day, while the latest matings were observed on 1 September 2002 among the snails collected on that day. None of the snails collected on 13 September 2003,

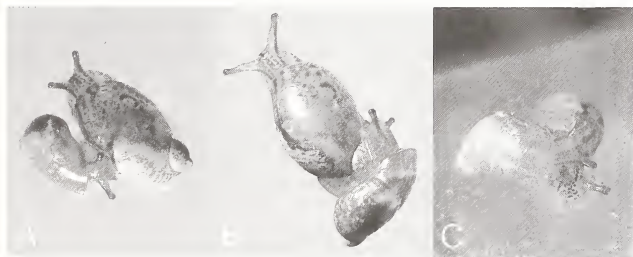


Figure 3. Courtship behavior preceding the mating of *Oxyloma retusum*. A, the smaller active snail is climbing onto the shell of the larger passive snail; B, the active snail is turning around the apex of the passive snail and moving towards the latter's head; C, having failed to initiate mating, the active snail is crawling across the head of the passive snail to repeat its cycle.

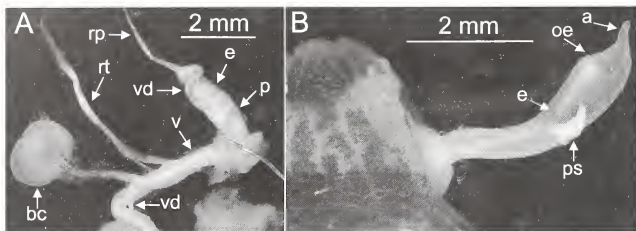


Figure 4. Lower genitalia of *Oxyloma retusum*. A, genitalia removed from a snail with the penis and the epiphallus still within the sheath; B, everted penis of a snail killed soon after mating. Abbreviations: a, appendix; bc, bursa copulatrix; e, epiphallus; oe, opening of epiphallus; p, penis; rp, retractor of penis; rt, retractor of tentacle; ps, possible paraspermatophore; v, vagina; vd, vas deferens.

25–26 October 2003, and 23 October 2004 mated in the laboratory.

Courtship (the sequential behavioral steps prior to mating) started when an active snail climbed on the shell of a passive snail (Fig. 3A). If the snail on top started out on the left side of the bottom snail, it crawled around the apex and then along the right side of the shell of the bottom snail towards its head (Fig. 3B). After the top snail reached the head of the bottom snail, either the snails started copulating or the top snail continued to crawl, first across the head of the bottom snail (Fig. 3C) and then along the left side of its shell towards the back. The top snail then crawled around the apex of the shell of the bottom snail one more time and back to its head to attempt to initiate mating again. The snails that could not initiate copulation were observed to circle their partners' shells two or three times before climbing down and leaving. In one case, an active snail took approx. 10 minutes to circle its partner's shell almost three times before they started mating.

A pair started copulating when the top snail twisted its head and brought its genital opening against that of the bottom snail (Fig. 1). After a pair started mating, the bottom snail stopped crawling and the snails remained motionless for the rest of their mating. During mating, the snails' tentacles were partially or completely withdrawn (Figs. 1–2).

Once the two snails' genital openings were closely pressed against each other, no external parts of their genitalia were visible and I could not ascertain if mating was anatomically reciprocal by looking at the close junction of the genital openings, even under magnification (Fig. 2).

Nineteen pairs of snails were separated during mating and forced to withdraw their penises. In 17 pairs, mating was anatomically reciprocal (Fig. 5). In the remaining two pairs, I could see only the penis of the top snail being withdrawn.

Therefore, I assumed that in those two pairs mating was anatomically unilateral.

On one occasion, I photographed two pairs mating simultaneously on top of each other. The examinations of the snails during mating and of their photographs later indicated that each snail was mating with only one other snail.

I timed the uninterrupted matings of 11 pairs at 19–21 °C. The median mating duration was 79 min (mean = 81 min) with a range of 63 to 97 min. At the completion of mating, the snails separated, the top snail climbed down and the snails crawled away from each other.

Significance of shell size

Casual observations indicated that the smaller snail in a mating pair was usually on top (Figs. 1 and 3). To support those observations, I measured the shell length and noted the position of each snail in 40 mating pairs (Table 1). When the shell length difference between the snails in a pair was 1 mm or less, the respective positions of the snails in each pair were not different than a random distribution (Chi-square test, $\chi^2 = 1.8$, $P = 0.180$). But when the shell length difference between the snails in a pair was more than 1 mm, the positioning of the smaller snail on top in all cases was significantly different than a random distribution ($\chi^2 = 20$, $P < 0.0001$).

Oviposition

I watched two snails while they were laying eggs in the laboratory. Prior to oviposition, a snail's head-foot outside its shell became swollen; the snail stopped moving and appeared moribund. One snail took approx. 41 minutes to lay 22 eggs. Five clutches from captive snails had 4 to 22 eggs. The eggs did not have hard shells but were enclosed inside a jelly matrix.

Annual population cycle

From April 2002 through March 2006, live *Oxyloma retusum* were abundant at both stations from early spring until the end of October. Snails were either on cattail stalks or on muddy areas next to the water. However, during the final season of field work in April and May 2008, casual observations indicated that the populations at both stations had decreased significantly although no physical alterations of the landscape were evident.

In contrast to their visibility and abundance from late March through October, the snails were rare and difficult to locate during the rest of the year. During the nine searches carried out between early November and early

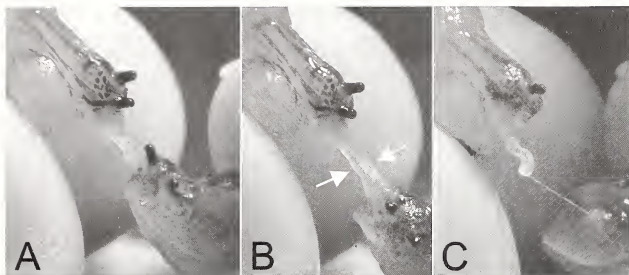


Figure 5. Forced withdrawal of the penises of a mating pair of *Oxyloma retusum*. A, the penises of both snails are still inserted into each other's vaginas; B, the snail on the right (bottom) has withdrawn its penis (right arrow), while the penis of the snail on the left (top) is still inserted (left arrow); C, the snail on the left has withdrawn its penis.

Table 1. Positioning of snails in mating pairs according to their shell sizes. There were 20 pairs in each size group.

Shell size difference (mm)	Smaller snail on top (# of pairs)	Larger snail on top (# of pairs)
≤1	13	7
>1	20	0

March from 2002 through 2008 lasting a total of about 3 hours, I found only five live *Oxyloma retusum*. Active snails between spring and early fall seemed incapable of withdrawing fully into their shells even when they were handled repeatedly. In contrast, all of the snails found in the winter were fully withdrawn into their shells and dormant. The edges of their apertures were loosely attached to dead plant material, such as tree or cattail leaves. The shell lengths of these five snails were as follows: 6.6 and 7.6 mm (10 November 2006), 4.2 mm (27 December 2005), 5.4 and 5.7 mm (12 January 2002).

The shells of the snails collected early in the spring usually had a flange-like ridge across their body whorls (Fig. 1), indicating that the aperture, normally thin and fragile in growing snails, had thickened prior to winter dormancy and formed what is referred to as a varix (Moore 1952). Out of a total of 57 snails collected on 4–5 April 2003, 38 had a prominent varix across their body whorls, while the rest had a less distinct varix.

The frequency distributions of the shell lengths from April through October for 2003 and 2004 are given in Fig. 6. The snails attained their largest shell sizes near the end of June. The largest snail encountered, on 13 June 2004, had a shell length of 14.1 mm. All of the snails larger than ~11 mm

disappeared by August and were presumed dead (Fig. 6). The smallest mating snail observed had a shell length of 6.2 mm. Therefore, I took 6 mm to be the arbitrary minimum shell length for sexually mature snails. Snails with shells 6 mm or longer made up more than 80% of the population in April and August (Fig. 6).

DISCUSSION

Some uncertainty remains about the identity of the snails despite the anatomical similarities between them and the published descriptions of *Oxyloma retusum* (Pilsbry 1948, Miles 1958, Franzen 1963, Wu 1993). The

primary reason for this uncertainty is that prior to Pilsbry (1948), species descriptions were based exclusively on shells, which not only lack distinct and species-specific features but also are variable (Franzen 1963). The subsequent anatomical studies have shown variability also of the reproductive organs of snails identified by different authors as *O. retusum* (Miles 1958, Franzen 1963, Wu 1993). One characteristic of *O. retusum* is its coiled epiphallus (Pilsbry 1948, Franzen 1963); however, both Miles (1958) and Wu (1993) noted that in some specimens the epiphallus was straight. One of the five snails I dissected also had a straight epiphallus. Likewise, the penis may also be straight or coiled (Miles 1958, Franzen 1963). Coiled penises were present in two of the five snails I dissected. Franzen's (1963) recommendation that anatomies of all described *Oxyloma* species be studied and compared with each other before we can determine which species are valid remains in effect today more than 45 years later.

The shell-mounted mating position of *Oxyloma retusum* is the same as those of other succineid species (Hecker 1965, Webb 1977b, Villalobos *et al.* 1995, Rundell and Cowie 2003). Webb (1977b) did not mention the circling of an active snail around the shell of its passive prospective mate that I observed during the courtship of *O. retusum*. Hecker (1965) reported a similar courtship behavior prior to mating of *Succinea putris* (Linnaeus, 1758) and suggested that the active snail's circling may stimulate the passive snail. However, as Hecker (1965) also noted, courtship does not always lead to copulation; I observed pairs of *O. retusum* separate after the active snail had circled its partner's shell two or three times.

Reverse-size-assortive mating observed in *Oxyloma retusum* (Table 1) has been noted in other succineids (Jackiewicz 1980). Jordans *et al.* (2005) also showed that the majority of the mating pairs of *Succinea putris* consisted of a

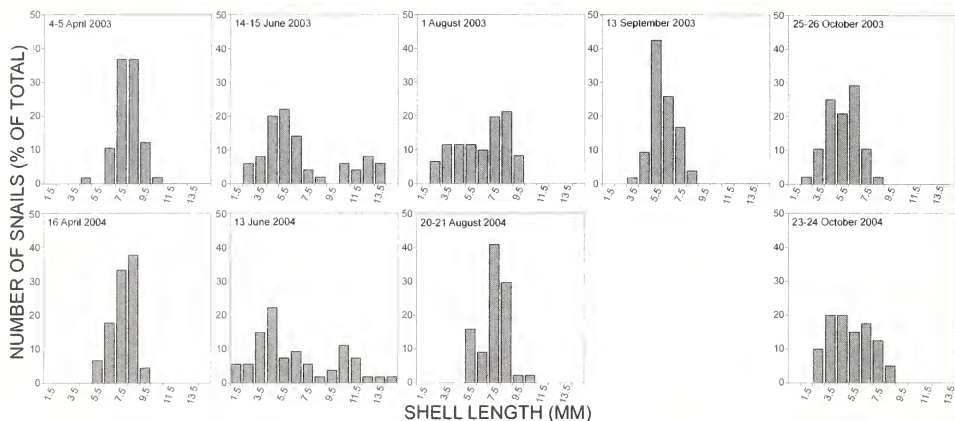


Figure 6. Frequency distributions of the shell lengths of live *Oxyloma retusum* from April through October for 2003 and 2004. Shell lengths are grouped in 1-mm classes.

small active snail and a large passive snail. Their explanation for this behavior, that it is easier for a larger snail to carry a smaller one than vice versa, especially on vertical surfaces, makes sense for several pairs of *O. retusum* that I observed mating vertically (Fig. 1) or upside down (Fig. 2). Mating between snails of unequal sizes requires that the active snail be able to judge, relative to its own size, the size of its prospective partner. Therefore, shell-circling during courtship, in addition to its possible stimulatory action, may also help an active snail compare its size with that of its partner.

Webb (1977b) gave a mean mating duration of 67 min with a range of 37 to 108 min for *Oxyloma retusum* at an unspecified temperature. In comparison, the mean mating duration measured in this study was 81 min (median, 79 min) with a range of 63 to 97 min at 19–21 °C. Hecker (1965) compared the copulation times of *Succinea putris*, *Succinea oblonga* (Draparnaud, 1801), *O. elegans* (Risso, 1826), and *O. sarsi* (Esmark, 1886). The copulations of *S. putris* lasted up to 8 hours, while the mean copulation times of the other three species were approx. 90 min (Hecker 1965, fig. 15). Jordaens *et al.* (2005) reported the median mating duration of *S. putris* at 20 °C as 487 min with a range of 230 to 725 min. The biological significance of the much longer copulation time of *S. putris* than those of other succineid species is unclear.

Eighty-nine percent of the interrupted matings of *Oxyloma retusum* were anatomically reciprocal. This agrees with Webb's (1977b) statement that mating between *O. retusum* was "mostly reciprocal," although, it is not clear from

Webb's account how many pairs of snails he had examined. As Jordaens *et al.* (2005) and Davison and Mordan (2007) noted, anatomical reciprocity during mating does not necessarily imply reciprocal sperm transfer. Nevertheless, Jordaens *et al.* (2005) showed that in *Succinea putris*, whose matings were also anatomically reciprocal, 86% of matings involved reciprocal sperm exchange. Therefore, they stressed that the active snail on top cannot necessarily be considered to be the "male" and the passive snail on the bottom the "female." Their findings, if extrapolated to my results, strongly suggest that in *O. retusum* reciprocal penis insertion also results in reciprocal sperm exchange and that each snail in an anatomically reciprocal pair performs both as a male and a female.

In contrast, Brown *et al.* (2003, 2006) noted that during the matings of the Hawaiian *Succinea thaauumi* Ancey, 1899 and *S. newcombiana* Garrett, 1857 the snails on top were "acting as the male," which, presumably, meant that the sperm exchange was unilateral. Brown *et al.* (2003) also reported one case of three individuals of *S. thaauumi* mating simultaneously with the middle snail "acting as both a male and a female." The only case of simultaneous mating of more than two individuals of *Oxyloma retusum* that I observed involved four snails on top of each other, but each snail mated with only one other snail.

The anatomy of the everted penis of *Oxyloma retusum* (Fig. 4B), including the subterminal opening of the epiphallus, agrees with Webb's (1977b) descriptions. The identity and the function of the granular, crystal-like formations on the surfaces of everted penises of *O. retusum*, also noted by Webb

(1977b), are unknown. Webb (1977a) proposed the term paraspermatophore for the “softer, non-preformed” masses of semen of succineids. He described the paraspermatophore of *Catinella avara* (Say, 1824) as a “short cylindrical spindle” that adhered to the everted penis and noted that the semen of *O. retusum* was likewise discharged as a paraspermatophore. Jackiewicz (1980) also noted that the spermatozoa of the European succineids formed a “compact mass” in the genitalia of preserved specimens and Jordaens *et al.* (2005) described the sperm package of *S. putris* as “cohesive but plastic.” These descriptions indicate that in succineids the discharged semen forms a recognizable mass that may indeed be conveniently referred to as the paraspermatophore. It is likely that the appendage attached to the everted penis of one of the *O. retusum* killed after copulation is a paraspermatophore (ps in Fig. 4B). The resemblance of the overall shape of the putative paraspermatophore to that of the appendix (a in Fig. 4B) suggests that the paraspermatophore was formed inside the tip of the everted penis as Webb (1977a) speculated.

The comparison of the frequency distributions of the shell sizes of *Oxyloma retusum* measured at the end of October 2003 and early in April 2004 (Fig. 6) indicates that very little, if any, shell growth takes place during the winter. The increase in the proportion of larger shells in April probably results from the rapid growth that starts in late March. This conclusion is supported by the observations that the five snails found during the November-February period were dormant and that their shell lengths (4.2–7.6 mm) were within the ranges of the October measurements. Furthermore, the presence of a varix across the body whorls of the shells of most of the snails in early spring indicates that growth stops during the winter.

The snails that survive the winter become sexually mature (shell length ≥ 6 mm) by the end of March and early April when they make up more than 80% of the population (Fig. 6). The snails continue to grow throughout the spring, reaching maximum shell sizes near the end of June when they start to die off. None of the winter-survivors seem to reach August. Their offspring (the spring generation) grows during the spring and the summer and apparently goes through a brief reproductive period near the end of August, giving rise to a summer generation. This is implied by the increase in the proportion of sexually mature snails at the end of summer and indicated by the appearance of very small (shell length ≤ 4 mm) snails in August and early September (Fig. 6). At the same time, the shifts towards smaller sizes observed in the histograms for September and October indicate that some of the snails making up the spring generation, presumably those that reproduce at the end of the summer, die during that period. In other words, the population goes through a partial turnover near the end of the summer and the survivors from the spring generation are

joined by the summer generation to create the group that goes through the winter dormancy to become the following spring's reproducing adults.

Pilsbry's (1948) comments regarding *Oxyloma decampi gouldi* (synonymized with *O. retusum* by Hubricht 1985), that he could find only half-grown shells in autumn and that most of the large individuals probably died by the end of summer, accord with the life cycle of *O. retusum* presented here. Strandine (1941) studied the life cycle of *Novisuccinea ovalis* in Illinois during one year and interpreted his data as showing that *N. ovalis* hibernated during the winter, reproduced the following spring, and died off by the early summer. Therefore, the annual life cycle of *N. ovalis* is also similar to that of *O. retusum*.

The data of Brown *et al.* (2003, 2006) show that growth, and to a lesser extent, reproduction are continuous throughout the year in the two species of semelparous Hawaiian succineids they studied. Likewise, Villalobos and Monge-Nájera (2004) noted that *Succinea costaricana* von Martens, 1898, also a semelparous species, had continuous growth and reproduction throughout the year in Costa Rica. In contrast, *Oxyloma retusum*, undoubtedly because of the much colder winters in Maryland than in southerly climates, goes through a dormant period between November and early March. Nevertheless, the northern and southern American succineid species all seem to have semelparous life cycles, despite the differences in their habitats and the climates they experience.

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